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1 Connecting Earth Observation to High-Throughput

2 Biodiversity Data

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54 **Preface**

55 There is much interest in using Earth Observation (EO) technology to track biodiversity,
56 ecosystem functions, and ecosystem services, understandable given the fast pace of
57 biodiversity loss. However, because most biodiversity is invisible to EO, EO-based
58 indicators could be misleading, which can reduce the effectiveness of nature
59 conservation and even unintentionally decrease conservation effort. We describe an
60 approach that combines automated recording devices, high-throughput DNA
61 sequencing, and modern ecological modelling to extract much more of the information

62 available in EO data. This approach is achievable now, offering efficient and near-real-
63 time monitoring of management impacts on biodiversity and its functions and services.

64 **Meeting the Aichi Biodiversity Targets**

65 From Google Earth to airborne sensors, the Copernicus Sentinels, and cube satellites,
66 Earth Observation is undergoing a rapid expansion in capacity, accessibility, resolution,
67 and signal-to-noise ratio, resulting in a recognised shift in our capability for using
68 remote-sensing technologies to monitor biophysical processes on land and water¹⁻³.
69 These advances are motivating calls to use Earth Observation products to manage our
70 natural environment and to track progress toward global and national policy targets on
71 biodiversity and ecosystem services⁴⁻⁶. Foremost among these policies are the Strategic
72 Plan for Biodiversity and the Aichi Biodiversity Targets, which were adopted in 2010 by
73 the Parties to the Convention on Biological Diversity (CBD) to "take effective and urgent
74 action to halt the loss of biodiversity in order to ensure that by 2020 ecosystems are
75 resilient and continue to provide essential services..."⁷. The United Nations Sustainable
76 Development Goals⁸ now include some of the Aichi Targets, and the 2015 Paris
77 Agreement has reiterated the commitments of the UN Framework Convention on
78 Climate Change to reducing emissions from deforestation and forest degradation

79 (REDD+) and to securing non-carbon benefits, which include biodiversity and ecosystem
80 services⁹.

81 However, we have struggled to track and report progress toward the Aichi Targets in a
82 standardised and comprehensive way¹⁰. Although almost two-thirds of the CBD Parties
83 have updated their National Biodiversity Strategies and Action Plans to reflect the 2010
84 revisions, many still do not contain measurable indicators on the state of biodiversity, let
85 alone ecosystem services. This lack of quantification conceals the impacts of policy and
86 management interventions on biodiversity and ecosystem functions and services¹¹. The
87 difficulty of designing indicators¹²⁻¹⁴ has prompted an international consortium of
88 biodiversity scientists called GEO BON (Group on Earth Observations' Biodiversity
89 Observation Network) to propose a framework of Essential Biodiversity Variables¹⁵, with
90 the aim of setting minimum standards of coverage to ensure informativeness and to
91 harmonise disparate local measures so that biodiversity and ecosystem data can be
92 compared over space and time. The Essential Biodiversity Variables thus measure the
93 'state of biodiversity' at multiple levels: genetic composition, species populations,
94 species traits, community composition, ecosystem structure, and ecosystem function¹⁵.

95 Although it was originally envisioned that most of the variables (genetic to community
96 composition) would be scaled up from "intensive *in-situ* measurements"¹⁵ taken on the

97 ground, such measurements are costly and difficult because they are traditionally
98 gathered by visual and aural detection of plants and animals in the wild (preceded by
99 months or years of observer practice) and by mass collection of organisms (followed by
100 months of identification from morphology), so that data collection is slowed by human-
101 caused bottlenecks in sampling and taxonomy¹⁶.

102 As a result, attention is now being focused on designing 'Satellite Remote Sensing-
103 Essential Biodiversity Variables' (SRS-EBVs) to enable cost-effective and global-scale
104 monitoring^{5,6,12}. The problem here is that only a few Earth Observation products can be
105 mapped directly to Essential Biodiversity Variables and then to Aichi Targets, because
106 these products primarily measure gross vegetation and landscape metrics, such as land
107 cover and phenology⁴. For example, Pettoirelli et al.¹² found only two Earth Observation
108 products (net primary productivity and fire incidence) that could serve as Essential
109 Biodiversity Variables for the Sahara, despite this biome's suitability for remote sensing
110 due to its visible biodiversity hotspots, remoteness, and availability of long time series.
111 Many of the Aichi Targets require data with species-level resolution, either because some
112 species are direct policy targets (e.g. Target 9: "invasive species controlled or eradicated")
113 or because species compositional data define the metric (e.g. Target 11: "protected areas
114 are ecologically representative and conserved effectively").

115 Clearly, a radically new approach is required if progress towards the Aichi Targets is to
116 be accelerated, one that is robust, widely affordable, and can record stocks and changes
117 in biodiversity and ecosystem services consistently, continuously, and at high resolution
118 over large geographic scales. Here, we present such an approach in a framework that
119 exploits recent efficiency gains and analytical breakthroughs in sensors, computation,
120 ecology, taxonomy, and genomics (**Figure 1, Box 1**).

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123 **Box 1. Inferring a Hidden Ecosystem Function from Space**

124 Large-bodied Amazonian monkeys are responsible for a key ecosystem function: they are
125 the primary dispersers of large seeds, which are associated with more carbon-dense tree
126 species. Peres et al.¹⁷ have proposed that this function boosts forest carbon storage. The
127 idea can be tested by using Earth Observation data and public records to map human
128 settlements and transport corridors and predict where monkey populations have
129 declined through hunting^{17,18}. We can then use on-the-ground sampling and airborne
130 sensors to test whether forests that have had longer exposure to hunting lack monkey
131 populations and have more low-carbon-density tree species dispersed by wind and birds.
132 In short, by combining Earth-Observation-derived maps of human activity with empirical
133 observations of the response of primate populations to that activity, it should be

134 possible to map and track an ecosystem function (large-seed dispersal) that is invisible to
135 satellites but contributes to an important ecosystem service (climate regulation).

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138 **From Point Samples to Continuous Maps**

139 Instead of trying to map Earth Observation (EO) products directly to biodiversity, as
140 encapsulated by SRS-EBVs^{4-6,12}, we propose to extract more information from EO data by
141 interpolating biodiversity point samples to build continuous landscape maps of species
142 distributions (**Figure 1**)¹⁹. Because it is species that are mapped, it then becomes possible
143 to layer on the vast biological knowledge that we have collectively built up over decades
144 of research, including historical distributions, phylogenetic relationships, and knowledge
145 of species traits and interactions to infer, map, and track the distributions of ecosystem
146 functions and services (**Box 1**). This approach, which we call here **CEOBE** (Connecting
147 Earth Observation to Biodiversity and Ecosystems), is possible because of (1) major
148 advances in EO sensitivity and capacity, (2) more efficient techniques to collect
149 biodiversity data on the ground, and (3) modern community-analysis models from
150 statistical ecology. We now review each of these advances, with additional detail in
151 Supplementary Information.

152 **The New Era of Earth Observation**

153 There are ten times as many satellites in operation now as there were in the 1970s, a
154 result of increasing sensor longevity and a six-fold increase in launches²⁰. Spatial
155 resolution has improved to less than 1 m in both optical and radar sensors. Data
156 continuity is also being maintained, most directly by the launch of NASA's Landsat 8 in
157 2013, which extends and technically enhances the 40-year Landsat record of medium-
158 resolution, multispectral surface observations²¹. Data continuity is a key factor in
159 understanding changes in biodiversity, as threats to biodiversity impact at a range of
160 scales and often across lengthy timespans²².

161 The long-term Landsat record is being enhanced by new satellite systems and multiple
162 sensors in a global network, a 'virtual constellation' that may help overcome problems in
163 terrestrial monitoring from single sensors². As part of the Copernicus program, the ESA
164 Sentinel satellites are the latest addition to the global network. With six missions planned
165 and the first three launched, the Sentinels have radar, optical sensors, radiometers, and
166 spectrometers with different goals²³. Sentinel-1, the radar satellite, and Sentinel-2, the
167 superspectral high-resolution mission, are of particular interest to biodiversity
168 monitoring, with long-term continuity of measurements, global coverage, and quick
169 revisit times ^{24,25}.

170 There have also been developments in hyperspectral sensors with EnMAP, HypsIRI,
171 PRISMA, and FLEX imaging spectrometer missions planned¹. In addition, airborne data
172 collection using high-resolution 3D airborne laser scanning is complementing spectral
173 information with structure²⁶. Swarms of commercial cube satellites and the use of drones
174 to carry sensors are additional significant steps that complement these large-scale
175 programs (**Supplementary Note 1** "Earth Observation technology").

176 The increase in spatial resolution in the new sensors implies greater precision because
177 reference measurements taken within meter-scale plots on the ground can be matched
178 directly to meter-scale pixels²⁷. This in turn improves the ability of EO to recognise
179 spatial gradients and boundaries.

180 Two additional factors affect the utility of remote sensing data for understanding
181 biodiversity change (**Supplementary Note 2** "Biodiversity and ecosystem information in
182 EO data"): affordability and access²². There has been a cultural shift, with free open
183 access on the rise. The opening of the Landsat archive in 2008 was a monumental
184 development²⁸, with ESA's Copernicus program following suit. Data access also refers to
185 the ability of users to retrieve, manipulate, and extract value from EO data. Cloud
186 computing and toolboxes are making these processes manageable, even with large data
187 archives.

188 The availability of copious EO data that have been shown in multiple studies to correlate
189 closely with on-the-ground measures of ecosystem structure, habitat condition, and even
190 animal communities (**Supplementary Note 2**) might suggest that remote sensors can be
191 used directly to define environmental indicators, but we must acknowledge that we are
192 still in the early stages of understanding how biodiversity delivers ecosystem functions
193 and services, and how they all respond to exogenous change. Directly observing
194 functional diversity is a partial solution but only with visible biodiversity such as
195 vegetation²⁶. Thus, the challenge is to find ways to exploit the high efficiency and
196 information content of EO data while not falling prey to *reification fallacy* (**Box 2**), which
197 can arise when convenient but incomplete indicators are made available^{29,30}. Our
198 institutions and reporting systems then retain the option to add and respond to new
199 knowledge.

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202 **Box 2. The Perils of Convenient Indicators**

203 If we rely too directly on EO data, we run the risk of *reification fallacy*, in which a mere
204 indicator of a policy target itself ends up the target. Reification fallacy can reduce or
205 narrow conservation effort³¹ and can crowd out future discoveries³². For example, while
206 remote sensing is an efficient and direct way to measure forest *cover* (Aichi Target 5:

207 reducing the loss rate of natural habitats), using forest cover and phenology to measure
208 the contribution of biodiversity to carbon stocks (Target 15)⁴ would ignore taxa invisible
209 to satellites and could thus result in policymakers failing to exert the additional effort
210 that is required to conserve saprotrophic fungal diversity, seed-dispersing mammals, and
211 the seemingly inconsequential isopod, all of which have been implicated in boosting
212 carbon storage^{17,33,34}. More generally, land-cover class, which is a common EO-indicator,
213 is a highly error-prone way to map and assess the complex processes supporting
214 ecosystem services³⁵. In short, convenient EO products could lead policymakers to focus
215 only on that portion of biodiversity and ecosystem services that is directly observed by
216 remote sensing, ignoring the rest.

217

218 **High-Throughput Biodiversity Measurement**

219 Most biodiversity, whether animal, fungal, plant, or microbial, and its many functions and
220 services, is invisible to EO and will remain so for some time. But a growing number of
221 efficient technologies are available for detecting and identifying biodiversity on the
222 ground^{36,37} (**Supplementary Note 3 "Biodiversity technology"**). Automated bioacoustic
223 and camera-trap recording devices (ARDs) can run continuously for weeks and
224 accumulate thousands of records of invertebrates, birds, fish, reptiles, amphibians, and

mammals, and thus allow extended sampling of large areas at low workloads³⁸⁻⁴².
Alternatively, high-throughput DNA sequencers can be used in metabarcoding or
metagenomic pipelines to detect and identify anywhere from one to thousands of
species at a time from mass-collected, bulk samples of organisms (e.g. 'biodiversity
soups'⁴³), or from 'environmental DNA,' which is DNA liberated into the environment in
the skin, hair, mucous, saliva, sperm, eggs, exudates, faeces, urine, blood, spores, root
fragments, leaves, fruit, pollen, or rotting body parts of their original owners^{44,45} (**Figure
2, Supplementary Note 3**). Multiple studies have now shown that metabarcode datasets
reflect high-quality, morphologically identified biodiversity datasets sufficiently closely to
allow correct management decisions, given best-practice protocols and controls⁴⁶⁻⁵¹.
The taxonomic identities, phylogenetic affinities, functional genes⁵², spectral properties
(of visible vegetation^{26,53,54}), and/or co-occurrence patterns⁵⁵ of the detected species can
be used to parameterise process-based production functions for ecosystem services⁵⁶⁻⁵⁸
(**Figure 1**). For instance, the species identities and biomasses of wild bees identified
metagenomically from bulk samples⁵⁹ could be combined with flower-use observation
data⁶⁰ and detailed vegetation classification from EO to infer the availability and nature
of local pollination services. Metagenomic data matched to identified species can be
particularly powerful when the impacts of species loss on ecosystem function are not

243 random, evidence that has previously relied on intensive field sampling, e.g. in tropical
244 freshwater⁶¹ and marine benthic communities⁶².

245 **Statistical Modelling as the Bridge**

246 Earth Observation technology can produce large-scale, fine-resolution maps and dense
247 time series of a wide range of biophysical variables (**Supplementary Note 1 and 2**), but
248 it is difficult to translate the biophysical variables into biodiversity information. In
249 contrast, ARDs and DNA sequencing are capable of generating large amounts of
250 biodiversity information at species- or even individual-level resolution^{63,64}, but only from
251 point samples (**Supplementary Note 3**). Modern methods of statistical modelling allow
252 us to interpolate these point samples to build continuous species maps and to estimate
253 emergent metrics such as richness and dissimilarity⁶⁵⁻⁶⁸, potentially also including
254 estimates of species abundance or biomass, depending on the sampling and analytical
255 methods used (**Supplementary Note 4** "Statistical modelling").

256 The three approaches with immediate potential are *Joint Species Distribution Models*⁶⁹⁻⁷²
257 (including *Latent Variable Models*), *Community Occupancy-Detection Models*⁷³, and
258 *Generalised Dissimilarity Models*^{65,74} (**Figure 3, Supplementary Note 4**). Each approach
259 starts with a site-by-species matrix, from data that have been collected by ARDs or been
260 generated via metabarcoding or metagenomics (**Figure 2, Supplementary Note 3**), plus

any existing species distribution data. If some species are not detected, repeat sampling can be used to infer missing occurrences⁷³. The site-by-species matrix is then paired with a corresponding site-by-environmental-covariate matrix, generated from continuous EO data plus any relevant geographical layers, and the two datasets are combined statistically to infer the joint distributions of multiple species across entire regions (**Figure 3, Supplementary Note 4**). All three approaches also provide a rigorous framework for quantifying sources of uncertainty and have already been applied successfully to conventionally acquired datasets (**Box 3**).

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271 **Box 3. Current Practice in Community Modelling**

Ovaskainen et al.⁷¹ used a joint species distribution model to predict the distributions of 55 butterfly species scored for presence/absence on a grid of 2609 10 X 10-km cells across Great Britain that had been sampled from 1995-1999 in a large citizen-science project. The model was successfully parameterised with a training dataset of just 300 cells and four environmental covariates (degree-days and three types of vegetation cover), plus spatially structured latent variables. Latent variables use observed species subgroupings to detect the effects of unmeasured environmental filters or species interactions such as competition. The parameterised model was used to predict butterfly

communities in the testing dataset, which consisted of the remaining 2309 grid cells. Together, the measured and latent variables explained an average of 42% of the variance in species occurrence (with medium-prevalence species more accurately predicted), and the two most dominant latent variables revealed a north-south gradient in species composition, with especially distinct communities in the southeast and northwest. Species richness per grid cell was accurately predicted, and the model's ability to discriminate presence and absence was high (mean AUC = 0.91).

Kéry and Royle⁷⁵ used community-occupancy modelling to analyse the 2001 Swiss breeding-bird survey while accounting for variation in detectability due to season, site, and species effects. The dataset consisted of 254 1-km² grid cells, each visited three times. The fitted model predicted each species' probability of occurrence as a function of site elevation and forest cover, as well as variance in the uncertainty of occurrence estimates, making it possible to estimate species distributions across the landscape and confidence in those estimates. Parameter estimates were naturally less precise for rare species, but information could be 'borrowed' from data-rich species to increase the precision of predictions for rare species. These procedures were able to compensate for the fact that only 134 total bird species had been detected in the survey, which is less than the true total of 163 species known to breed regularly in Switzerland, plus 22

occasional residents (the testing dataset). The occupancy-corrected model estimated that between 1 and 11 species had been overlooked per grid cell and thus, that the true total in 2001 was 169 species.

Mokany et al.⁷⁶ applied Generalised Dissimilarity Modelling (GDM) to a dataset of 2330 expert surveys of New Zealand land snails, which recorded 845 of 998 known species. The GDM was parameterised with a training dataset of 2280 surveys and fourteen environmental variables and explained 57% of the variation in beta diversity. In addition, a generalised additive model parameterised on the training dataset explained 27% of the variation in species richness (after scaling the 20 x 20-m survey quadrats to match the area of modelling units (200 x 200-m); see discussion of scaling in **Supplementary Note 4**). Finally, the outputs were combined using a procedure called DynamicFOAM to assign snail species to communities across New Zealand. Error was assessed by predicting compositions in a testing dataset of 50 sites that had been held out of the model. On average, the model was able to predict half the species that had been observed in each cell, and the predicted total occupancy area per species was highly correlated with the number of quadrat occurrences (Pearson's $r = 0.902$). When quadrats were pooled into groups of 3 to 400 to reduce sampling stochasticity, predicted species richnesses almost perfectly explained observed richnesses ($R^2 = 0.99$).

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318 By mapping species distributions as the primary output, we do not lock ourselves into an
319 arbitrary set of convenient indicators, and ongoing discoveries on the relationship
320 between biodiversity and function, which are typically carried out at the species level, can
321 be added. As an illustration, the species diversity of wood-decaying fungi in natural
322 forests is notoriously difficult to assay but can be predicted in part by the volume and
323 species diversity of the stock of dead wood on the ground⁷⁷, and these environmental
324 covariates are partially quantifiable via airborne LiDAR sensors (**Supplementary Note**
325 **1**)⁷⁸, thus allowing EO-based inference of the distribution and level of wood-decaying
326 fungal diversity. Subsequent and unrelated research has suggested that pieces of dead
327 wood inhabited by a higher diversity of fungal species decompose more slowly, possibly
328 due to more intense interference competition³⁴. Combining the two results suggests that
329 an EO-derived map of fungal species diversity could be used to contrast landscape
330 management options for how well they conserve saprotrophic fungal biodiversity and
331 thus enhance carbon storage.

332 Two further reasons for focusing on species-resolution maps as the primary output are
333 that the regional species pool (*gamma diversity*) and the biological dissimilarity of sites

334 (*beta diversity*) could contribute to maintaining functional stability^{58,79,80} and that species-
335 resolution outputs retain the option of aggregation to represent different aspects of
336 biodiversity, including higher-taxonomic, functional, and phylogenetic groupings⁸¹.

337 Many methods are also available to predict *individual* species ranges, and EO can help
338 improve their accuracy, as shown by an example⁸² combining MODIS satellite data with
339 environmental DNA to map an invasive diatom over a watershed [Target 9, invasive
340 species pathway identified] (**Supplementary Figure 3.1**). However, ecosystem functions
341 and services are rarely delivered by only one species, and simply summing the outputs of
342 individual models to simulate communities is computationally inefficient, statistically
343 flawed, and does not account for species interactions⁸³.

344 **From CEOBE to Aichi**

345 In essence, our argument is that new technologies make the new community-modelling
346 approaches (**Box 3, Figure 3**) widely feasible, especially in biodiversity hotspots, where it
347 is particularly difficult to generate large datasets. Larger numbers of environmental
348 covariates and species together increase explanatory power by providing a greater
349 breadth of predictors, and by exploiting latent variables and letting rare species 'borrow'
350 information^{42,75,84}, respectively. As a result, continuous streams of EO data can be more
351 powerfully interpreted to track biodiversity status and trends (**Figure 1**).

352 The predictive performance of fitted models can be cross-validated by rounds of
353 comparison with testing datasets that were either split from the model-training
354 dataset^{71,76} or derived from historical and expert knowledge⁷⁵, and thus, the adequacy of
355 the input data and sampling design, or conversely the degree of model uncertainty, can
356 be assessed *post hoc* (**Box 3**). The regularly updated biodiversity maps that are the
357 primary outputs of the CEOBE approach (**Figure 1**), plus the quantified uncertainty in
358 those maps, can then be incorporated into a larger process of structured decision
359 making and adaptive management⁸⁵⁻⁸⁷ to (1) identify likely consequences of proposed
360 actions by observing natural experiments that mimic those actions, (2) compare observed
361 results of management interventions against objectives, and (3) help identify and tackle
362 sources of uncertainty.

363 An early example of the CEOBE approach is given by Sollmann *et al.*⁴², who used
364 community-occupancy modelling to connect environmental covariates from the 5-m-
365 resolution RapidEye satellite to point-sample data from camera traps in three tropical-
366 forest logging concessions in Sabah, Malaysian Borneo, one of which has been managed
367 to reduced-impact-logging standards set by the Forest Stewardship Council (Aichi Target
368 7, sustainable management under forestry). The dataset consisted of detection events for
369 28 mammal species at 166 camera-trap stations, each station scored using EO data for

370 distance to water, distance to oil-palm plantation, and forest condition. Estimated
371 relationships between species occurrence and the three covariates were used to predict
372 species occurrence across the three reserves, with rare mammal species borrowing
373 information from more common ones. Species richness was estimated to be higher in
374 the FSC-certified reserve, particularly for threatened species (Target 12, improved
375 conservation status of threatened species). The percentage of area occupied, which could
376 indicate larger population sizes, was also estimated to be higher in the FSC-certified
377 reserve for the majority of species, including for some highly endangered species like the
378 Sunda pangolin *Manis javanica*. Finally, the modelled species richness maps were found
379 to correlate strongly with EO-estimated aboveground biomass at the large spatial grain
380 of whole reserves, but not at a finer resolution (potentially due to hunting at reserve
381 borders), further demonstrating the critical contribution of ground-level point samples
382 for linking pure-EO data to biodiversity.

383 The major remaining components of uncertainty relate to generalisability, because only a
384 single FSC-certified reserve was sampled; the applicability of results to arboreal species,
385 which tend to be detected more frequently in forests with disturbed canopy but are not
386 necessarily more widespread in these forests; and wide confidence intervals around
387 parameter estimates for some species as a consequence of sparse data and a fairly

388 complex hierarchical model. This example serves as a proof of concept that camera
389 trapping and occupancy modelling can be used to assess biodiversity conservation based
390 on species maps, and the approach has been incorporated in the ten-year forest
391 management plan and wildlife monitoring strategy for the FSC-certified area. Repeated
392 surveys will help to narrow uncertainties in the model, and a future power analysis is
393 planned to estimate the sampling effort required to detect trends and/or provide
394 estimates with a desired level of certainty⁸⁸.

395 Another example of the CEOBE approach is the use of Generalised Dissimilarity
396 Modelling to connect EO-derived metrics of habitat degradation and fragmentation^{89,90}
397 to over 300 million records of more than 400,000 species from the Global Biodiversity
398 Information Facility (www.gbif.org) and the Map of Life (mol.org)⁹¹. The GDM models
399 spatial turnover in biodiversity composition at 1-km-resolution globally, and by invoking
400 the assumption that terrestrial biodiversity declines according to the classical species-
401 area power function, the GDM estimates the proportion of biodiversity that has been
402 retained in each grid cell after habitat loss, based on the proportion of similar habitat
403 remaining unimpacted within the landscape⁹². This metric thus tracks whether rates of
404 loss, degradation, and fragmentation of natural habitats are being reduced (Aichi Target
405 5). Further, by combining this approach with a global database of protected-area

406 coverage (www.protectedplanet.net), it is possible to report progress against Target 11,
407 which aims for protected areas to cover areas of particular importance to biodiversity
408 and ecosystem services and to be ecologically representative and connected (see also
409 Ref. 93). An important caveat is that the biodiversity data in this case are historical in
410 nature and thus contain the taxonomic and sampling biases and constraints of the past
411 (**Box 2**). Ideally, the biodiversity data will transition to up-to-date, properly sampled, and
412 more taxonomically comprehensive point samples.

413 Of course, CEOBE outputs cannot contribute to all Aichi Targets, namely those that are
414 focused on policy, planning, and funding reform (Targets 2, 3, 4, 20), the conservation of
415 genetic cultivars (Target 13), the alleviation of climate-change pressures on coral reefs
416 (Target 10), benefits sharing (Target 16), and the integration of traditional knowledge
417 (Target 18). It also remains to be seen how well or poorly EO data reflect biodiversity in
418 aquatic ecosystems (Targets 6 and 11), although environmental DNA on its own is a
419 highly promising source of data on aquatic biodiversity. On the other hand, the efficient
420 production of biodiversity maps and open access to analytical pipelines will help to
421 disseminate the science base and technologies related to biodiversity (Target 19), and
422 could contribute to public awareness of efforts to conserve biodiversity (Target 1) and
423 improve the efficiency of national biodiversity planning (Target 17).

424 **Conclusions**

425 It is extremely difficult to identify all the species present in a location (*the Linnaean*
426 *challenge*), to delimit the geographic distributions of species (*the Wallacean challenge*),
427 and to quantify their responses to natural and anthropogenic environmental change (*the*
428 *Hutchinsonian challenge*)⁹⁴. A synergy of Earth Observation, automated recording
429 devices, high-throughput DNA sequencing, and modern statistical modelling can meet
430 these challenges by making it possible to scale up from data-rich but finite sets of point
431 samples to spatially continuous biodiversity maps, which are more informative than a few
432 convenient indicator species but still let us generate summary statistics to communicate
433 trends to decision-makers and the general public. The use of formal statistical
434 frameworks lets us quantify error, identify gaps in our understanding, objectively rank the
435 most likely pressures on biodiversity from multiple candidates, and increase the
436 robustness of change detection. Adding information on species interactions and
437 functions helps link biodiversity to ecosystem functions and services (**Box 1, Figure 1**) in
438 a process-based approach⁵⁶, rather than relying on crude estimates from land classes³⁵.
439 Finally, as DNA-based technologies mature, the same samples could track population-
440 genetic diversity^{64,95,96}.

441 A global, multi-resolution monitoring network is thus within our reach but will still
442 involve a number of challenges associated with technical capacity, computation and data
443 storage, and data standardisation. For every ecologically distinct region, there will be an
444 initial cost to collect data for model parameterisation, followed by a low level of
445 continuous sampling, which will be necessary for updating models and for surveillance
446 monitoring of environmental drivers that are invisible to EO, such as broad-spectrum
447 insecticides. The initial costs are probably best borne by governments, as part of their
448 commitment to the Convention on Biological Diversity, and there is great promise in
449 using citizen-science networks to collect standardised, bulk biodiversity samples over
450 large areas. A laudable example is the School Malaise Trap Program that recruited
451 hundreds of secondary-school science classes to collect arthropods across Canada
452 (malaiseprogram.com). Initial investment could also come from existing monitoring
453 budgets with the expectation that additional information content will compensate for
454 reduced sample numbers within existing programs⁸². The follow-up continuous sampling
455 requires steady funding streams, and the standardisation of the CEOBE approach meets
456 the needs of international certification schemes, such as REDD+, Climate, Community &
457 Biodiversity Standards, Forest Stewardship Council, and the Roundtable on Sustainable
458 Palm Oil, which all require the continuous monitoring of biodiversity and ecosystem

459 services. Biodiversity-offset payments to mitigate the impacts of development and
460 carbon emissions are also expected to provide funding streams, and standardised
461 assessments are needed to ensure that offsetting results in biodiversity net gain⁹⁷.

462 The CEOBE approach also depends on institutional support for the multidisciplinary
463 collaborations needed to generate, combine, analyse, and act upon data from disparate
464 disciplines (EO, ARDs, genomics, taxonomy and systematics, ecosystem functions and
465 services, statistics, and decision science), expertise that no single individual has^{12,30,98}.

466 Identifying causal determinants of species distributions needs a clear understanding of
467 phylogenetic structure and functional diversity, the ecological processes involved, and
468 what EO sensors can and cannot observe⁹⁹. Expert knowledge will also contribute to
469 sampling design and covariate selection so that the full breadth of environmental
470 conditions is captured, especially those not visible to EO.

471 On the other hand, collaborations need not be global. Political and social interests will
472 vary by region, and agencies should be encouraged to trial CEOBE within their
473 jurisdictions where there are clear opportunities to improve management, while also
474 enforcing the publication of primary data and analytical pipelines^{27,100}. The
475 Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) could play an
476 important role as a global coordinating institution.

477 Resources for environmental management are always likely to be limited, but by doing
478 more with our expensively gained field data, we can take action more efficiently and
479 effectively. What is required now is leadership by governments and international
480 organisations to stimulate integrated research and to endorse the use of comprehensive
481 biodiversity information⁶.

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486 **Author Contributions**

487 BC and HB led the sections on Earth Observation technology. KB and DWY led the
488 sections on Biodiversity technology. AB led the sections on Statistical modelling. AB, RS,
489 AW, OO, and DWY led the sections on case studies (Box 3 and CEOBE to Aichi). CM led
490 the Conclusions section. Figures were created by KB, AB, CC, and AZ. All authors
491 contributed to multiple rewrites, with a large contribution by DR. AB and DWY wrote the
492 first draft and supervised the work.

493 **Additional Information**

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495 **Competing Interests**

496 DWY and AV are co-founders of a private company that provides commercial
497 metabarcoding services.

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798 **Figure legends**

799 **Figure 1. CEOBE – Connecting Earth Observation to Biodiversity and Ecosystems. Top**

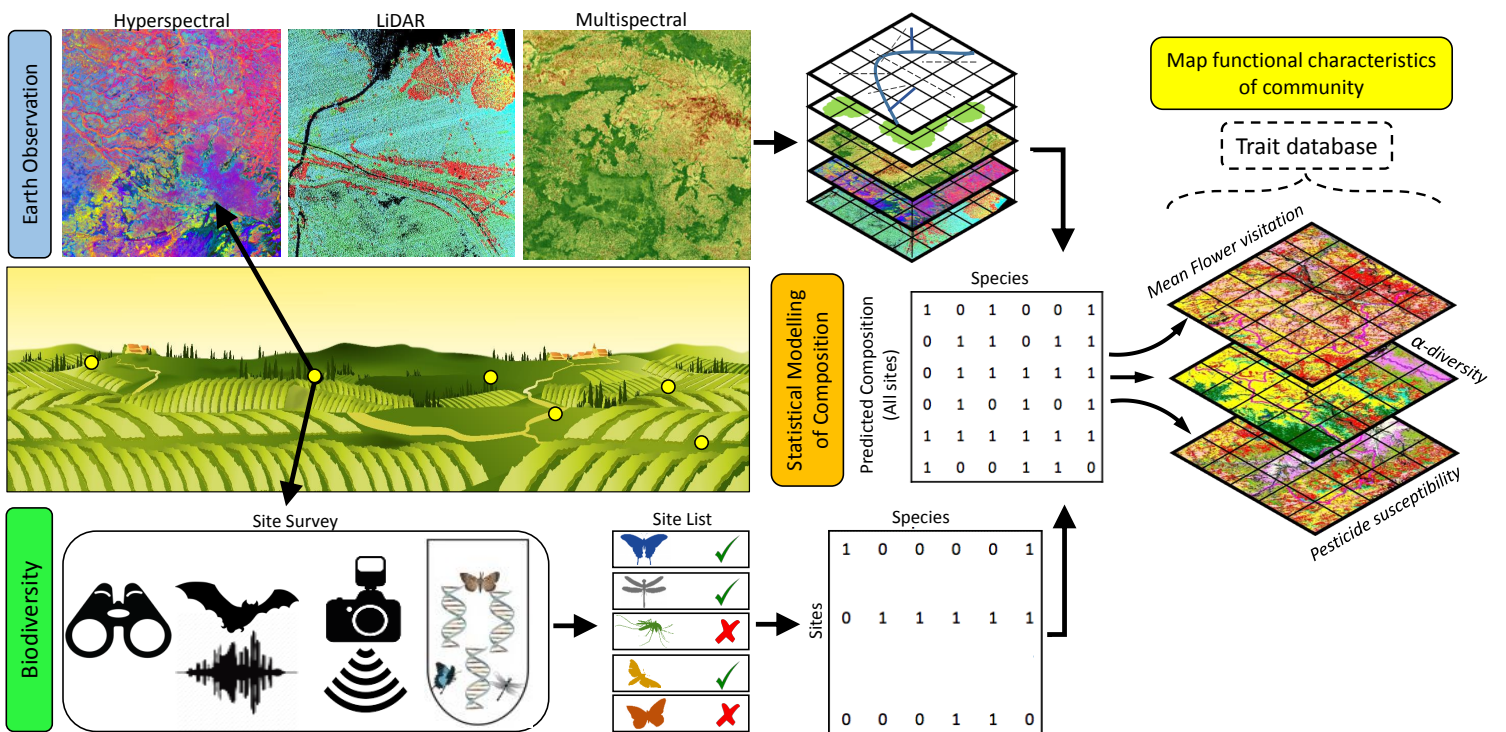
800 **row left:** EO data and other geographical datasets are used to generate spatially
801 continuous maps of biophysical data (**S1, S2**). **Middle row left:** A real landscape with
802 point-sample locations indicated by yellow dots. **Bottom row left:** Biodiversity is
803 recorded manually using traditional methods, automated audio or image recording
804 devices, or metabarcoding or metagenomic pipelines to generate a site X species table
805 (**Figure 2, S3**). However, most of the landscape is not sampled (empty rows in the table).
806 **Right side:** The point samples are combined statistically with continuous biophysical
807 maps to predict biodiversity composition over the whole landscape (**S4**). In combination
808 with ancillary data like trait databases, process-based models can then identify the
809 functional composition of any location and map the expected distributions of ecosystem
810 functions and services.

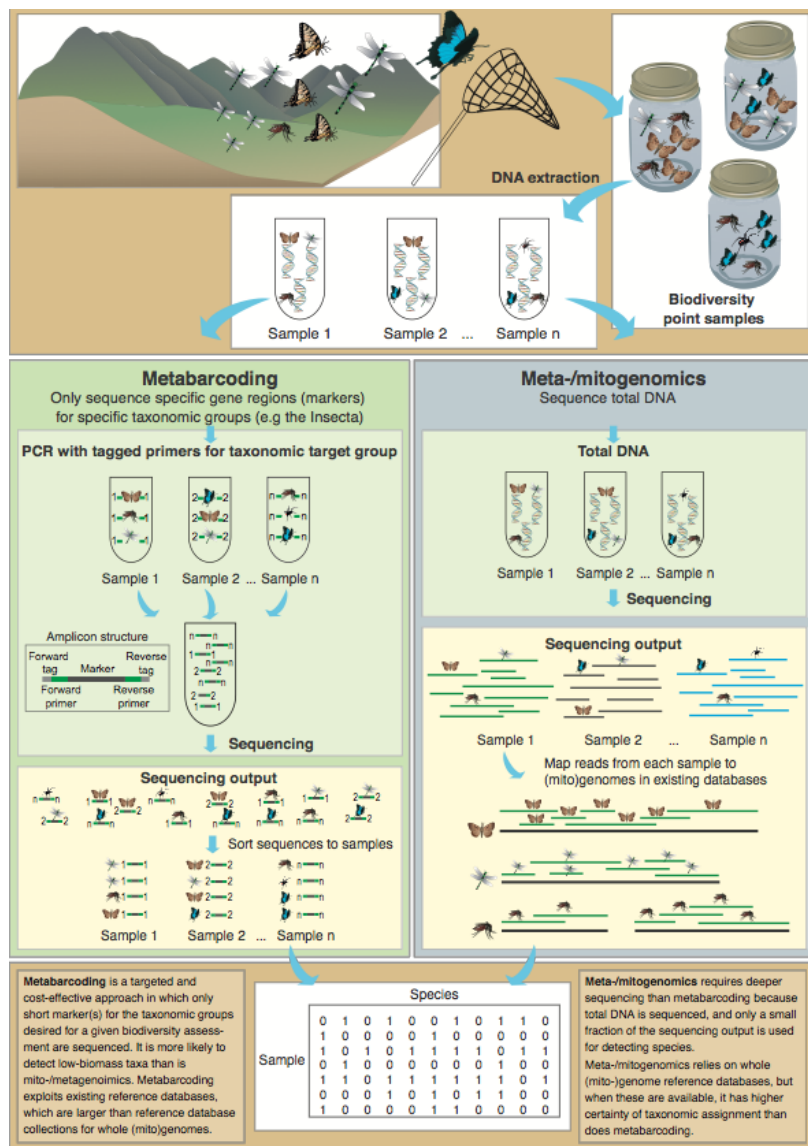
811 **Figure 2. Metabarcoding and metagenomic processing pipelines for high-throughput**

812 **biodiversity surveys. Top row:** Point locations across a landscape are sampled for
813 biodiversity, and DNA is separately extracted from each sample. Three common sample
814 types are (i) bulk samples of arthropods (depicted here), (ii) environmental DNA (eDNA)

815 from soil, water, and air, and (iii) invertebrate collectors of vertebrate DNA (iDNA), such
816 as mosquitoes, leeches, flies, dung beetles, and ticks. **Left column:** Metabarcoding –
817 Each sample's DNA is amplified via PCR (polymerase chain reaction) for a particular
818 marker gene that is taxonomically informative, the samples are pooled and sequenced
819 on a high-throughput sequencer, and then sorted back to sample by the sample-specific
820 tags added during PCR. The sequences are then clustered into Operational Taxonomic
821 Units (OTUs), which are species hypotheses, and assigned taxonomies by matching
822 against online databases. **Right column:** Meta/mitogenomics – Each sample's total DNA
823 is sequenced, and the output DNA reads are matched to reference genomes, which are
824 often mitochondrial genomes. **Bottom row:** The output of both processing pipelines is a
825 'sample X species' table. Metabarcoding pipelines are useful for general biodiversity
826 discovery and surveys because online barcode databases are more taxonomically
827 complete, and even without taxonomic assignment, it is possible to calculate community
828 metrics from OTUs only. Metagenomic pipelines are more costly, but advantageous when
829 it is important to reliably identify particular sets of species and to a greater extent
830 preserve relative biomass information. See **S3** for further details. Clip-art courtesy of the
831 Integration and Application Network, University of Maryland Center for Environmental
832 Science (ian.umces.edu/symbols/).

833 **Figure 3. Three statistical pathways to map community composition and summary**
834 **metrics from the combination of biodiversity point samples and continuous Earth**
835 **Observation (EO) maps.** Local diversity – α , species turnover – β , and regional diversity –
836 γ . For clarity, the figure only considers models for species occurrence (OCC), not
837 abundance. GAM: Generalised Additive Model. DynamicFOAM is described in Ref. 76.
838 See **S4** for further details.



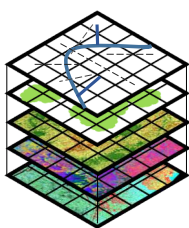


Joint Species Distribution Models / Latent Variable Models

Biodiversity point samples

EO Spatial covariates

Sites	Species					
	1	0	0	0	0	1
	0	1	1	1	1	1
	0	1	0	0	0	1
	0	0	0	1	1	0



$$OCC = f(\text{Site covariates}) + f(\text{Latent Variables})$$

Species distributions are described as a function of unobserved latent factors as well as observed covariates. Account for species covariance, but do not easily account for differences in species detection.

Predicted probabilities of species occurrences at all sites

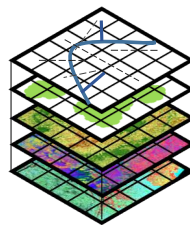
Sites	Species						Site Richness
	1	0	0	0	0	1	
	0	1	1	0	1	1	
	0	1	1	1	1	1	
	0	1	0	0	0	1	
	1	1	1	1	1	1	
	0	0	0	1	1	0	
Site matrix of dissimilarity (β)							Regional Richness α

Occupancy-Detection Models

Biodiversity point samples with repeated surveys

EO Spatial covariates

Sites	Species					
	1	0	0	0	0	1
	0	1	1	1	1	1
	0	1	0	0	0	1
	0	0	0	1	1	0



Site covariates

Survey covariates

$$OCC = \text{Occupancy.model} * \text{Detection.model}$$

Environmental covariates can describe both a species' distribution and how that distribution is observed, which itself can depend upon survey characteristics. Account for imperfect detection, but treat species independently.

Predicted probability of species occurrence at all sites (including unobserved species)

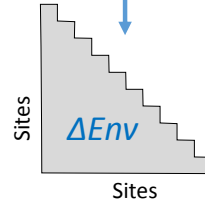
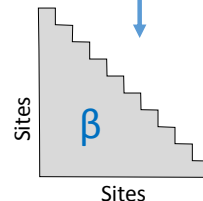
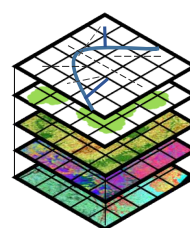
Sites	Species						Site Richness
	1	0	0	0	0	1	
	0	1	1	0	1	1	
	0	1	1	1	1	1	
	0	1	0	0	0	1	
	1	1	1	1	1	1	
	0	0	0	1	1	0	
Site matrix of dissimilarity (β)							Regional Richness α

Generalised Dissimilarity Models

Biodiversity point samples (high species diversity)

EO Spatial covariates

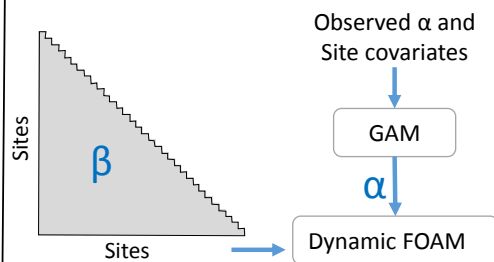
Sites	Species									
	1	0	0	0	0	1	0	0	1	0
	1	1	0	1	1	1	0	1	0	0
	0	0	0	0	1	1	0	0	0	1
	0	1	0	0	0	0	1	0	1	0



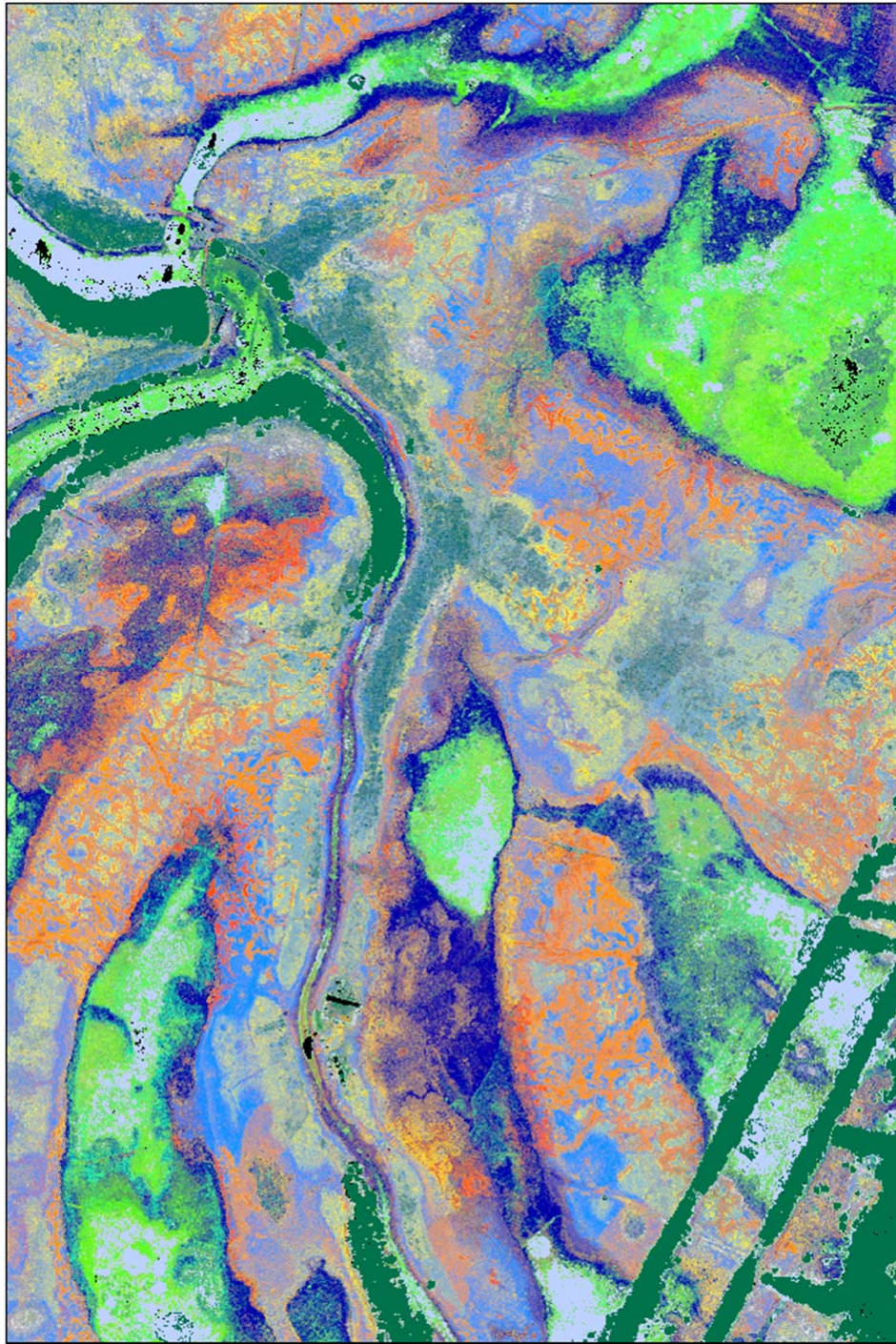
$$\beta_{ij} = f(|Env_i - Env_j|)$$

Compositional dissimilarity (β) between each pair of sites (i and j) is a function of the difference in environmental conditions (ΔEnv).

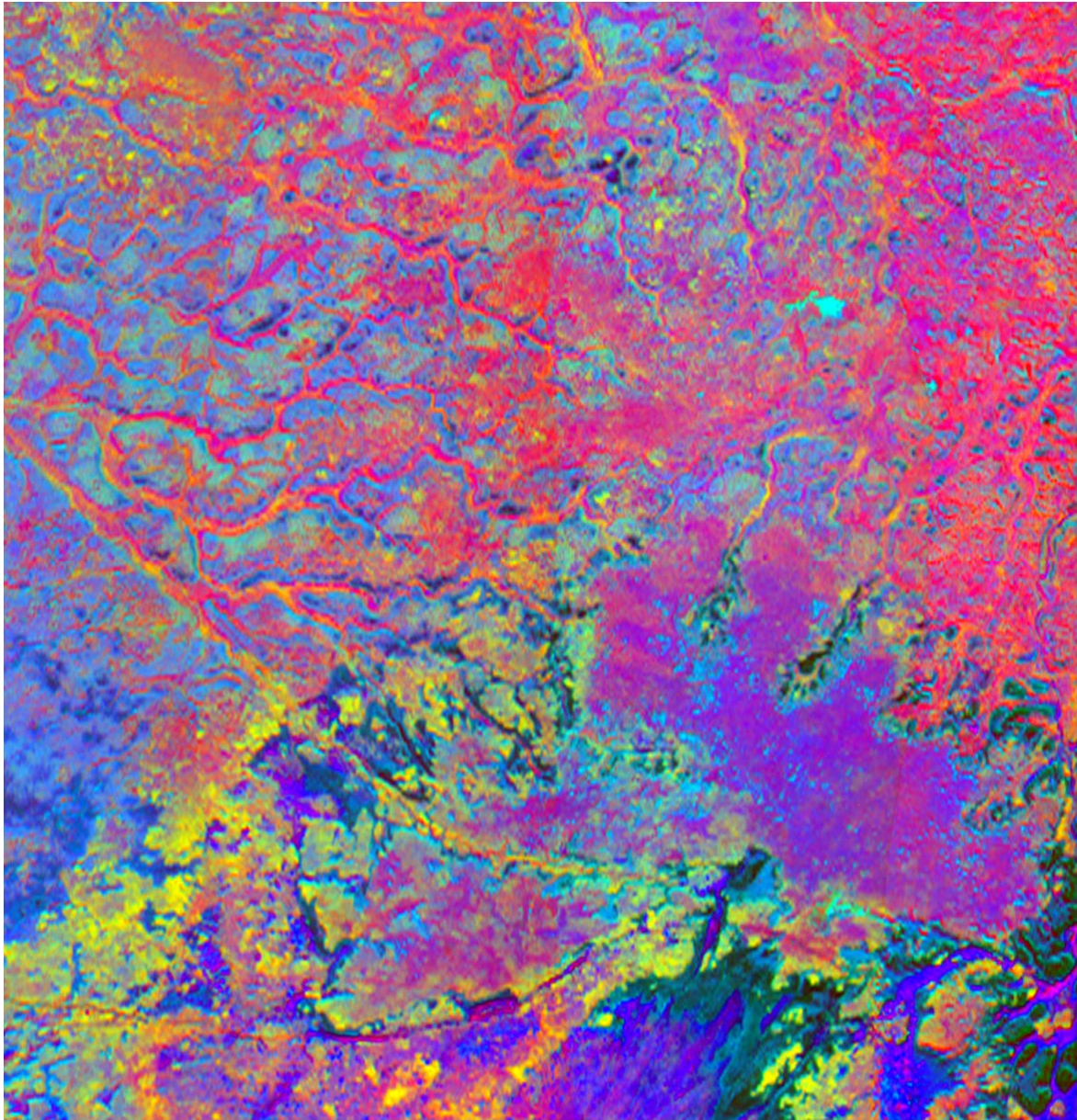
Predicted compositional dissimilarity between any pair of sites (β)



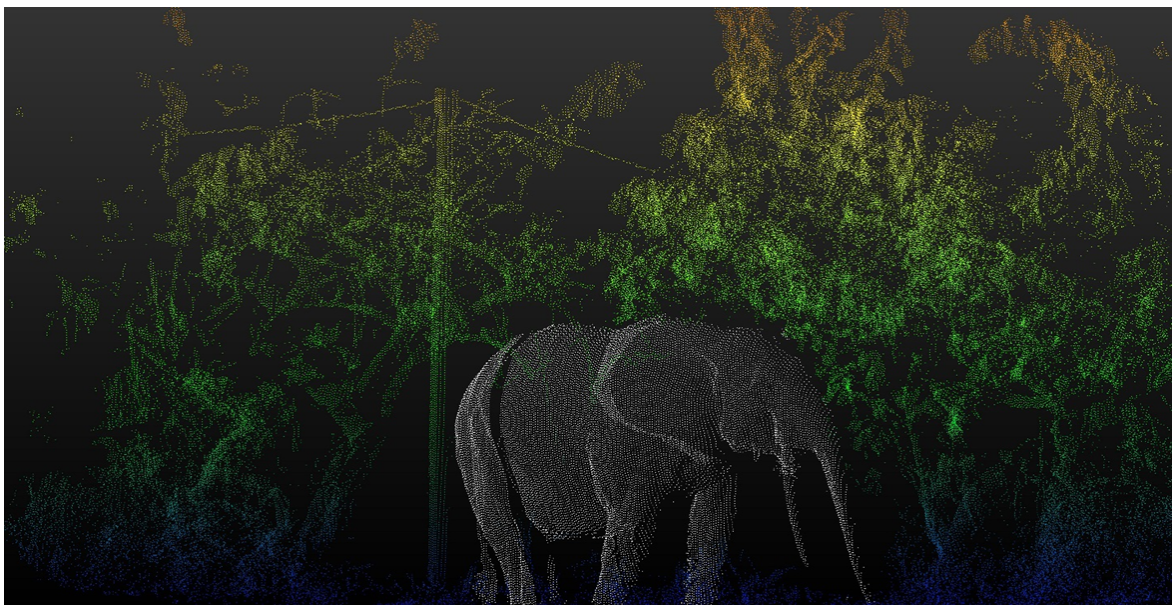
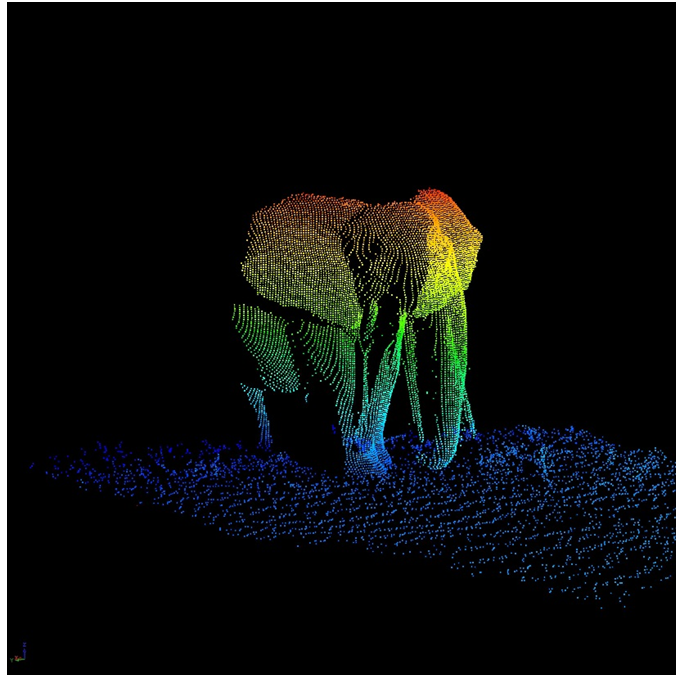
Predicted composition of all sites consistent with patterns of α and β



Fuzzy classification of grassland vegetation in an alkaline grassland in Püspökladány, Hungary, based on airborne LIDAR. Colours represent the weighted probability for a given vegetation class in each cell (0.5m²) (photo credit: András Zlinszky).



Vegetation composition of a peatland using Partial Least Square Regression models on a hyperspectral image. The image is a false colour composite showing the predicted abundance of Graminoids (Red), Shrubs (Green), and Bryophytes (Blue) (photo credit: Beth Cole).



A forest elephant “scanned” during a terrestrial laser-based measurement of a tropical rainforest in Gabon 2013 (photo credit: Kim Calders).

Connecting Earth Observation to High-Throughput

Biodiversity Data: Supplementary Information

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Supplementary Note 1. Earth Observation Technology

Earth Observation (EO) sensors can be differentiated into active and passive types. Active sensors direct their own source of electromagnetic radiation at the Earth and receive the signal reflected back from the target (e.g. Synthetic Aperture Radar, SAR, transmits microwave pulses). Passive sensors rely on external radiation sources such as the Sun (optical and thermal sensors fall into this category). Different sensors record

electromagnetic radiation in specific ranges of the electromagnetic spectrum, with wavelengths from 400-700 nm (visible light) to 700-2400 nm (near to shortwave infrared), 3000-14000 nm (thermally emitted radiation), and 1 cm-1 m (microwave radar wavelengths). Passive EO instruments record radiances at sensor, which generally have to be corrected for atmospheric aerosol and water vapour impacts in order to estimate the land surface reflectances from which EO-derived metrics are usually extracted. Active radar sensors record the transmitted energy that is scattered back from the surface, and since microwaves penetrate clouds, they provide an all-weather observing capability. However, longer wavelengths such as L-band (15-30 cm) and P-band (30-100 cm) can be affected by fluctuations in the total electron content of the ionosphere and the Faraday rotation. Optical and radar sensors are available from both airborne platforms (drones, aircraft) and spaceborne platforms (polar orbiting and geostationary satellites, international space station). Important characteristics of an EO sensor are its spectral coverage and spectral resolution (which bands of the electromagnetic spectrum it measures and at what wavelength detail), its spatial resolution (pixel size), and temporal repeat-frequency (number of days between two acquisitions at the same location). Many applications do not require frequent acquisitions, but multiple images can for instance help account for artefacts and error due to cloud cover¹.

Light Detection and Ranging (LiDAR) is an active remote-sensing technique that transmits infrared or visible polarised light and records the intensity and temporal delay of the received signal. Because of the constant speed of light in air, airborne LiDAR can measure the vertical height of objects with very high accuracy². Radar interferometry from tandem satellite constellations can also measure vertical height but is not as accurate as LiDAR and has a coarser spatial resolution than airborne LiDAR³. LiDAR systems can be imaging LiDARs or profiling LiDARs, and some systems record the full waveform of the received radiation, allowing the study of vegetation canopies in great detail, while others only record

the first and last return of the waveform. LiDAR instruments are usually mounted on airborne platforms (aircraft, drones) or used as terrestrial instruments (mounted on a tripod or used as a handheld device), with the exception of the spaceborne ICESAT-GLAS profiling LiDAR and the planned GEDI mission to be mounted on the International Space Station.

Supplementary Note 2. Biodiversity and ecosystem information in EO data

The spatial and temporal coverage of EO cannot be matched by *in-situ* surveys, and mapping of habitat extent and land cover types has therefore been incorporated into national EO-monitoring programs for many years^{4,5}.

Aboveground biomass and carbon storage – Forest ecosystems play a crucial role in global biogeochemical cycles, and deforestation has been a major contributing factor to increasing anthropogenic carbon emissions. Global initiatives such as REDD+ (Reducing emissions from deforestation and forest degradation, and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries) has been negotiated by the UNFCCC for years and was reiterated in the Paris Agreement⁶. While the main aim is to mitigate climate change by reducing carbon emissions, for which developing countries receive results-based payments, safeguards and non-carbon benefits (NCBs) are recognised, including consistency with the conservation of natural forests and biodiversity^{7,8}. The success of REDD+ therefore depends on our ability to accurately quantify the global distribution of carbon sources and sinks, for which EO such as SAR or LiDAR are now being developed⁹.

Airborne LiDAR can quantify forest canopy height and complexity, and understorey density over large areas, and has been particularly useful in forestry¹⁰. Although individual trees can

be mapped by very high pulse densities¹¹, forest structure is more commonly described by the heights of a lower density point-cloud aggregated over a forest plot. The average parameters for that forest can then be used to estimate aboveground biomass, which can be translated to ecosystem services like carbon sequestration and storage¹². Hollaus *et al.*¹³ demonstrated that even simple models could make accurate predictions of timber stock in alpine forests after being calibrated with inventory plot data ($r^2 > 0.80$). The study also showed model accuracy was not sensitive to LiDAR point density or the season of acquisition.

Although performance is likely to vary among habitat types, with accuracy usually greater in low diversity systems, and dependent on the number and size of calibration plots, a meta-analysis of more than 70 studies by Zolkos *et al.*¹⁴ found airborne LiDAR to be more accurate than radar or passive optical data. Yet more accurate estimates of carbon stocks may be possible using hyperspectral to discriminate tree species¹⁵. LiDAR can also be used in ecosystems other than forests. For example, Zlinsky *et al.*¹⁶ demonstrated that LiDAR can replicate ground-based multi-parameter assessments of habitat conservation status in a Natura 2000 grassland reserve in Hungary (Overall Accuracy=0.8); and using EO, the entire reserve could be surveyed.

Biodiversity – While the main focus of REDD+ is to reduce carbon emissions, there is also great potential to improve predictions of spatial patterns of biodiversity from vegetation structure. As argued elsewhere in this paper, these relationships could prove critical to achieving the ambitions of initiatives like REDD+ without compromising the benefits for biodiversity conservation¹⁷.

For instance, early EO products like NDVI (normalised difference vegetation index) have been shown to approximate changes in vegetation structure and hence turnover of the invertebrate ground fauna^{18,19}, and more recently high spatial resolution airborne imagery

has been shown to identify canopy gaps that are associated with the diversity of understorey vegetation²⁰. Spectral traits of plants are determined by their physiological and morphological traits, and there are demonstrated applications using EO to reveal the distribution of vegetation types^{21,22}, functional types²³, richness²⁴, and temporal changes²⁵ to name but a few²⁶. Nonetheless, the success of habitat mapping varies with habitat type, and research into the right combination of sensors and algorithms is ongoing²⁷⁻²⁹. Finally, the combination of hyperspectral sensors and LiDAR provides an extremely detailed picture of the Earth's surface, potentially capable of identifying the composition of individual trees in some landscapes³⁰ and reproducing patterns of tree richness and turnover in highly diverse rainforests at landscape scales^{22,31,32}. Eventually, similar measurements that directly observe or predict the distribution of biodiversity could be extended globally as satellite-based LiDAR and hyperspectral imaging systems become operational (**S1**).

LiDAR-derived structural metrics have also proven useful as predictors in many *animal* groups^{33,34}, and LiDAR could be more cost-effective than traditional methods for censusing invertebrate communities³⁵ and is likely to perform even better once taxonomic uncertainties are reduced with DNA-based identification³⁶.

Supplementary Note 3. Biodiversity technology

Automated Recording Devices (ARDs)

The first set of technologies encompass ARDs, such as camera traps and bioacoustic recorders that can be left in even remote field locations for weeks to months, capturing records of birds, amphibians, and mammals, and thus allowing continuous sampling of tens of thousands of hectares at a time, with occasional fieldwork to maintain sensors and retrieve data.

Camera traps. - Camera traps are powerful tools for detecting medium to larger-sized mammal species, particularly in forests³⁷, and they have also been used to study ground-dwelling bird species^{38,39} and lizards⁴⁰. Camera traps readily detect rare and cryptic or nocturnal species, and once set up, operate independently of an observer until battery life or memory capacity is exhausted. Early models used film roll cameras and active sensors, where an infrared beam was established across a potential animal path, and the unit was triggered when that beam was broken. Set-up of the infrared beam (height, positioning) had to be tailored specifically to the target species, and early studies often focused on the demography of single charismatic species such as tigers^{41,42}. Even with passive heat-in-motion sensors, which made for a more flexible set-up because of the increased area over which animals can be detected, the low number of exposures on film rolls was a severely limiting factor to the time that camera traps could be left in the field without revisiting.

The development of a wide range of digital models in the last 10 years has greatly expanded the applications of camera traps. With increasingly capacious memory cards and batteries, cameras can now routinely be left unattended for weeks up to several months (depending on the expected amount of animal traffic). Options for infrared flash make the equipment nearly invisible, even at night, reducing theft. Modern camera traps capture images of sufficient quality to allow identification to species in 80-90% of photos. Rapid sequential triggers of video options further increase the likelihood of obtaining the footage needed to identify species and individuals. Whereas the up-front investment in the equipment can be high (depending on manufacturer and specifications, a single trap can cost anywhere between \$80 and \$800), camera traps have repeatedly been shown to beat other methods (e.g. transects, track plates) in their efficiency to document medium to large terrestrial mammal species⁴³⁻⁴⁵, and they become more cost effective for longer surveys⁴⁴.

Although the method is still used to study the demography of individual species, particularly those with natural coat patterns allowing individual identification⁴⁶⁻⁴⁸, camera traps are now

also used in behavioural studies⁴⁹ and to study species interactions in space and time^{50,51}. Moreover, camera traps are increasingly used to survey terrestrial⁵²⁻⁵⁴ and even arboreal mammal communities⁵⁵⁻⁵⁷. Camera traps have been proposed as a tool in systematic biodiversity assessments in the context of biodiversity co-benefits of forest management certification and REDD+ payments⁵⁸. As an example application, a recent study on mammalian communities in Bornean forest reserves revealed that particularly threatened species benefit from sustainable forest management practices, applied in the context of certification by the Forest Stewardship Council (FSC)⁵⁴. Similarly, such standardised camera-trapping surveys, if repeated over time, can be used to monitor population and biodiversity trends, which would be impossible using traditional, observer-based fieldwork techniques.

How readily camera traps detect certain species is a function of many factors, including the species' behaviour and abundance, and the specific location and setup of the camera traps^{59,60}. For example, arboreal species are harder to detect with ground-based cameras than terrestrial species, and if cameras are set up preferably along roads and trails, species that use these trails will be detected sooner and more frequently than species that prefer to move through vegetation. Comparing biodiversity inventory data across sites and/or years therefore requires a standardised study design, and application of analytical methods that account for these differences in detectability (see Occupancy Modelling, below).

Bioacoustic sensors. - Species that produce acoustic signals can further be surveyed with standalone bioacoustic sensors⁶¹. Taxonomic groups most frequently studied with bioacoustic methods include birds^{62,63}, bats^{64,65}, anurans⁶³, certain insects^{66,67}, and cetaceans⁶⁸. Bioacoustic recordings have also been used to study fish⁶⁹, and non-flying mammals such as forest elephants⁷⁰ and primates^{71,72}. Using calls to detect and identify species has a long standing history in bird studies⁷³. Handheld sound recorders are a useful tool in such surveys to create permanent records of species audio-detections and to allow

for later identification (or verification) of records by specialists. There also exist standalone bioacoustic sensors⁷⁴ that, similar to camera traps, can be set up in the field to collect audio information without an observer's presence. Also similar to camera traps, they are primarily limited by battery and storage capacity, and storage capacity has increased dramatically with the switch from analogue to digital equipment⁶³. Automatic digital recording systems can be programed to record continuously or at certain times, or, alternatively, more advanced equipment can be triggered by calls above a certain amplitude or of a certain frequency spectrum^{75,76}.

Once recorded, calls/songs can be identified directly by a trained human observer (but of course only if the species produces a sound that is audible to humans) and/or by visualisation. The latter depicts species-specific acoustic parameters such as the temporal structure and frequency composition of a call/song. Most frequently, visualisation takes the form of a spectrogram, which shows the evolution of the frequency structure of a call over time, using color-coding for changes in amplitude⁷⁵. Such visualisation can reveal call characteristics that the human ear might not perceive. Call-matching to species based on these characteristics can be performed manually, or using computer algorithms. Obrist *et al.*⁷⁵ report that most automated identification software packages achieve a 90% recognition rate but can rarely be expected to cover all species present in a sample. Conversely, Russo and Voigt⁶⁵ have voiced concern over the accuracy of automated species identification of bat calls.

Criticism notwithstanding, advances in the development of audio-recorders and call-matching software make automated devices a promising tool for biodiversity inventory and monitoring⁵⁸. Such surveys, however, require extensive preliminary studies to compile reference call data bases. Similar to genetic reference libraries, there are now multiple available sound libraries (e.g. <http://www.ibac.info/links.html#libs>, accessed 8 Dec 2016), but especially for species-rich tropical communities, bioacoustic databases are currently

limited⁷⁷. Circumventing the need for species identification, some studies have suggested the use of bioacoustic diversity as a measure in and of itself. Rather than identifying individual calls and species, this approach is based on measuring the acoustic entropy (i.e. temporal and frequency heterogeneity) of entire soundscapes, and, on the assumption that there is competition for sound niches in time and frequency, a more complex soundscape is taken as an index for a more diverse community⁷⁸. Such bioacoustics diversity indices have been shown to correlate with taxonomic and functional diversity in birds⁷⁹ and are a promising field of study, albeit in need of further development and testing⁸⁰.

As with other survey methods, detectability and identifiability of individuals and species can be influenced by their vocalisation and other behaviour, habitat, weather, time of day, or the sensitivity of the recording equipment. For example, wind and concurrent vocalisation by other species were found to have a negative impact on the ability to identify frog calls⁸¹, and different equipment has been shown to result in different numbers of bird species detected⁸². In addition to false negatives (i.e. failing to record a species even though it is present), misidentification of calls can result in false positives⁸³. As such, standardised surveys and appropriate analytical methods are required to ensure comparability of results across space and time. Occupancy models, for example (discussed below) were developed to account for false negatives and can be adjusted to account for false positives as well^{84,85}. They have been successfully used in combination with automated acoustic monitoring⁸⁶.

DNA-based methods

Almost all DNA-based techniques exploit the stylised fact that some DNA regions exhibit higher levels of sequence difference between species and low levels of difference within species, which can be used to tell species apart. For animals, the best known of these so-called 'DNA barcodes' is a 658-nucleotide portion of the mitochondrial cytochrome oxidase subunit I gene, or COI, which taxonomists have used to build an online reference database

that links sequences to species (boldsystems.org, accessed 11 Oct 2016)⁸⁷. Other mitochondrial markers can also be used for taxonomic assignment, and these are available in online databases such as GenBank (blast.ncbi.nlm.nih.gov, accessed 11 Oct 2016). An organism can thus be assigned a taxonomic identification by extracting its DNA, amplifying it with a primer set for the chosen marker(s), sequencing these, and comparing them to a DNA reference database. Even if a species is not represented in a database, its congeners or confamilials usually are, allowing at least higher-level taxonomic identification.

When going from DNA barcoding of single specimens, as described above, to using DNA in synoptic biodiversity surveys, the major challenge is the need to assign taxonomic names to mixed samples containing DNA from multiple taxa, such as occurs in soil, water, faeces, and bulk insect samples. The rise of high-throughput sequencing platforms now makes this routine, and three major approaches are now being used: metabarcoding, high-throughput individual barcoding, and meta/mitogenomics.

Metabarcoding. – DNA is extracted from bulk or environmental samples containing DNA from a mix of different taxa, and a taxonomically informative marker like COI is PCR amplified using a universal primer set targeting the taxonomic group of interest (**Fig. 2** Main Text). In this way, only DNA markers of interest are sequenced, making this a cost-effective approach. The resulting sequences are then clustered into self-similar sets of sequences, each known as an Operational Taxonomic Unit (OTU), which is a species hypothesis. A representative sequence is taken from each OTU and assigned a taxonomy using an online database. The main output of metabarcoding is the classic ecological table of sample X species (OTU), but now achievable for at least hundreds of species across hundreds of samples, plus, to a lesser extent, their phylogenetic relationships. Metabarcoding data thus carry information on species co-occurrence at an unprecedented scale for joint-species-distribution modelling.

Metabarcoding relieves the taxonomic bottleneck, and it also helps relieve the sampling bottleneck. Firstly, metabarcoding can be applied to taxa such as meiofauna and dipterans that are easy to collect and ecologically informative but are so difficult to identify morphologically that they have been ignored in conventional surveys. Secondly, metabarcoding allows difficult-to-find species, such as fungi, fish, and terrestrial vertebrates, to be detected directly from microscopic bits of tissue that can be filtered out of soil, water, air, and parasites, known as 'environmental DNA' or eDNA^{88,89}. For instance, leeches, flies, mosquitoes, dung beetles, and ticks retain trace amounts of DNA from their previous meals on animal hosts or faeces, so mass invertebrate trapping could be used to survey other wildlife⁹⁰.

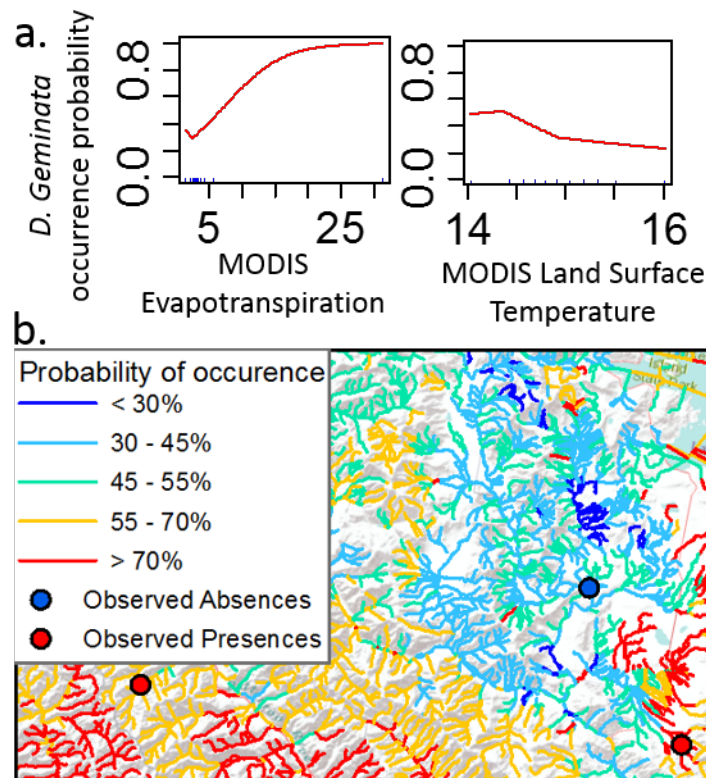
However, metabarcoding unavoidably introduces error, including *inter alia* taxonomic uncertainty due to e.g. PCR and sequencing error and incomplete reference databases, sample cross-contamination, and loss of species, biomass, and abundance information. Judicious sampling and primer design, lab practice, and bioinformatic and statistical pipelines are able to correct or compensate for these errors, and studies have shown that metabarcoding datasets reflect on-the-ground reality sufficiently closely to allow correct management decisions⁹¹⁻⁹⁶. It is worth noting that errors are explicit and quantifiable in DNA-based pipelines, whereas conventional surveys contain important error sources, such as visual misidentifications⁹⁷, that are essentially impossible to quantify or correct retrospectively.

High-throughput individual barcoding – In this method⁹⁸, large numbers of organisms, typically insects, are *individually* extracted, amplified, and tagged during amplification. Hundreds of individual amplicons are then pooled and sequenced, producing a separate barcode for each organism. Throughput is lower and workload is higher than in metabarcoding, but abundance information is preserved, and individual organisms can be revisited for further taxonomic study.

Meta/mitogenomics – Like metabarcoding, metagenomics can be used on bulk or environmental samples, but instead of targeting a specific gene, all DNA is sequenced, and the output datasets are interrogated *in silico* for taxonomically and functionally informative gene sequences (**Fig. 2** Main Text). Compared to metabarcoding, the advantage of this genomic approach is that it does not require a PCR amplification step to enrich target taxa, which should reduce bias. If samples are sequenced deeply enough, even low-biomass species can be detected in the mix (although sequencer library construction still imposes some biases). Metagenomics also preserves more information on species relative biomasses (a proxy for ecosystem-function importance), can reduce the risk of sample contamination, and depending on the number of samples, can reduce workload. Lastly, it increases the certainty of taxonomic assignment for species that are present in reference database. Currently, metagenomics is routinely applied to microbial communities but is not yet applied to Eukaryotes, due to their much larger genomes and thus higher costs. However, bioinformatic approaches that allow rapid pairwise comparisons of genomic datasets⁹⁹ and continued decreases in sequencing costs will make this approach feasible for Eukaryotes. That said, because orders-of-magnitude fewer species have been genome-sequenced, relative to barcode databases, metagenomics applied to Eukaryotes is best suited for studies that focus on hundreds of target species or fewer, for which it is possible to build custom reference databases.

In mitogenomics, the focus is on mitochondrial genomes, which can be individually assembled out of low-coverage sequencing of bulk samples ('genome skims'), even though mitochondrial reads typically make up <1% of a sequencer's output¹⁰⁰. This greatly reduces the cost of building reference databases. Mitogenomics has been used to reconstruct the phylogenetic community structure of soil-dwelling beetle communities¹⁰¹ and to reliably assign bee species to samples, even after the samples had been DNA-cross-contaminated by handling¹⁰².

Single-species detection – Finally, in situations where it is imperative to detect particular species of concern (e.g. early detection of invasive species or monitoring threatened species) with high probability, older molecular techniques can be used and/or added to the above methods. Species-specific primers can be used in addition to generic primers during metabarcoding to increase detection probability¹⁰³, or species-specific quantitative PCR (qPCR) can be conducted on eDNA samples. Although low throughput, this application of targeted qPCR reduces false negatives, provided that proper lab procedure, including negatives controls, is followed¹⁰⁴. Improved detection rates lead to improvements in model performance, thus increasing the reliability of the predicted distributions of these species of concern, and greater cost efficiency¹⁰⁵. Single-species detections using qPCR have been combined with MODIS satellite observations to build maximum-entropy species distribution models that predicted the distribution of an invasive diatom (*Didymosphenia geminata*) across the Rocky Mountains (Fig S3.1¹⁰⁶). Models based on occurrence data from both eDNA and traditional methods correctly predicted occurrence of *D. geminata* at external validation sites with a 93 – 100% correct classification rate (area under the receiver operating characteristic curve, a combined measure of sensitivity and specificity, ranged from 0.94 to 1.00). Temporally concurrent environmental predictors, including evapotranspiration or land surface temperature data from MODIS, allow these models to account for spatial and temporal variation and produce robust predictions (Fig S3.1a). This provides natural resource managers spatially explicit and extensive predictions on where this invasive species is likely to occur. The same approach is also being applied to mapping distributions of six native fish on the north-slope of Alaska to aid in their conservation¹⁰⁶.



Supplementary Figure 3.1 a: Relationship between MODIS measurements of evapotranspiration and land surface temperature and the occurrence of the invasive diatom *D. geminata*. b: Resulting maps of probability of *D. geminata* occurrence from applying model to individual stream segments.

Supplementary Note 4. Statistical modelling

Occupancy Detection Models – Logistical constraints dictate that a site-by-species matrix can only ever comprise a finite set of point samples, leaving most of the environment unsampled. Moreover, even within sampled sites, an unavoidable problem is false negatives: species that are indeed present but not detected^{107,108}, and in some cases false positives (species detected that are in fact absent). To correct for imperfect detection, occupancy-detection models are used to disentangle the factors that determine the occurrence of a species from those that affect the probability of detection, given occurrence¹⁰⁹. To estimate the probability of detection, a location is repeatedly sampled, either by spatially sub-sampling a site, or by re-visiting the same location multiple times

within a short time period. A hierarchical generalised linear mixed model (GLMM) – technically a zero-inflated logistic regression of species detection/non-detection data – is then used to predict the probability that a species occurs at a site, based on the site’s environmental covariates and the empirically estimated probability of detection, which can also itself be a function of site- and time-specific covariates.

Community Occupancy Detection Models – In the simplest application of occupancy detection, each species is considered independent, so a multi-species model simply combines the species’ environmental responses and their different detectabilities, and calculates metrics of diversity either from occupancy probabilities (in a likelihood framework, richness is the sum of all occupancy probabilities at a site), or from realised occupancy states (in a Bayesian framework, richness is the number of species estimated to occur at that site)^{110,111}. However, if the environmental responses of multiple species follow a common distribution, community occupancy detection models allow individual coefficients to be modelled as a random effect, whereby the data-poor species borrow information from data-rich species^{112,113}, which allows information on species traits to be included as predictors¹¹⁴. Furthermore, based on differences in species detection probabilities, occupancy models can also estimate the number of species that were never detected, by introducing zero-inflation within the inputs (“data augmentation”^{115,116}), recently extended for multi-region comparison¹¹⁷. More complex models can include the effect of community dynamics on spatial and temporal variation in occurrence¹¹⁸.

Joint Species Distribution Models / Latent Variable Models – An extension of the single-species approach is to consider all pairwise co-occurrences among species¹¹⁹. These so-called joint species distribution models (JSDMs) predict multi-species responses by not only modelling species-specific responses to environmental covariates as random effects but also accounting for residual patterns of co-occurrence not explained by environmental factors¹²⁰. In the past, the number of taxa that J-SDMs could consider was limited because

the number of parameters in unstructured variance-covariance matrices rises rapidly¹²¹. However, JSDMs can now analyse high numbers of species by inducing correlation among taxa using ‘latent’ unobserved factors¹²⁰. Residual correlation might indicate species interactions, like competition or predation, unmeasured predictors, spatial autocorrelation, or misspecification of the model, all of which warrant further investigation¹²². Spatially explicit latent variables allow one to predict a species community for a focal site using as predictors not only the environmental variables measured at the focal site, but also the occurrences and co-occurrences of the species in nearby sites¹²³, thus providing a statistically efficient tool for producing interpolated species distribution maps from sparse data on species rich communities. In principle, detection probability itself could also be included as a layer describing the observation process¹²⁴⁻¹²⁶. LVMs are currently an area of active research, and there has been rapid progress to expand computational limits and integrate with the breadth of previous development using hierarchical mixed models¹²⁰. Of particular interest is the opportunity to cluster species responses to environmental covariates according to species traits (i.e. “the fourth-corner problem”¹²⁷) making it easier to translate compositional turnover to functional shifts¹²⁸.

Generalised Dissimilarity Models – Finally, in very diverse communities with hundreds or thousands of taxa (e.g. soil fauna), it might not be meaningful to model the responses of individual species. Instead, generalised dissimilarity models (GDM) use a pairwise matrix of compositional dissimilarity to predict the nonlinear response of compositional turnover to environmental changes; weighting and transforming environmental variables so that conversion of multidimensional environmental space best describes the scaled turnover of biological composition¹²⁹. GDM can help identify new sampling sites for more reliable prediction¹³⁰, and uncertainty in variable selection can be further evaluated using Bayesian bootstrapping¹³¹. The dissimilarity matrix can also be derived from other biological distance metrics like sequence reads, allelic turnover, functional differences, or phylogenetic

diversity^{99,132,133}. The link between turnover of composition or function can then be tested using scaled environmental variables as predictors of spatial or temporal changes in service provision¹³⁴.

GDM has already been incorporated into EO-based applications to estimate ecological values at landscape scales^{135,136}, and model performance improves when combined with multispectral EO sensors¹³⁷. By predicting the dissimilarity of sites alongside an expected species-area relationship, GDM can also be used to estimate the proportion of biodiversity retained regionally (**Box 3** in main text). This has numerous conservation applications (e.g. protected areas effectiveness – Aichi Target 11¹³⁸), as well as quantifying the biodiversity left regionally (gamma diversity) to support ecosystem services¹³⁹. If the identity of species composition is still desired, GDM can be combined with a model of alpha diversity to estimate the probable species composition of every cell in a landscape¹⁴⁰. Furthermore, ecological processes like dispersal, growth rates, and metacommunity dynamics have been incorporated to predict ecosystem function and to rank management actions^{134,141}.

Sampling design. – For a given sampling effort, careful survey design can improve the accuracy and reliability of biodiversity models. For example, although we may be interested in the different species assemblages that each contribute to carbon storage in forests (e.g. large frugivorous mammals, isopods, and saprotrophic fungi; **Box 2** in main text), we would not sample for these disparate taxa at the same spatial grain¹⁴². For example, within the home range of a single monkey troupe, the composition of saprotrophic fungi might exhibit high levels of turnover across wood from different tree species. Fungi thus need to be sampled at a finer spatial grain than do mammals, and soil fauna might need to be sampled even more finely again. The grain of sampling should therefore try to match the grain at which environmental heterogeneity creates different habitats, but for efficiency, should also aggregate across points whose composition only varies due to stochastic fluctuations. Once the scale of analysis has been chosen, the sampling strategy can be adjusted to

ensure that biological samples represent an equivalent area effectively. For example, how many soil cores need to be sequenced to estimate the diversity of fungi within a forest plot? Scaling relationships like species-area curves can be a useful shortcut to compare community-level characteristics (alpha or beta diversity), but they cannot identify which species were missed. Instead, the differences in sampling effort, including the area sampled (e.g. number of quadrats), could be accounted for explicitly by species' detectability in community occupancy models¹⁰⁹. Finally, it is important that samples capture the full range and variability of environments across the region of study, especially where environmental differences lead to higher turnover¹³⁰. This is particularly true of finite resources that become limiting, such as soil moisture gradients that determine vegetation succession in arid biomes, but are less important to predicting turnover in the wet tropics. These decisions can be guided by expert opinion and existing survey data, but pilot studies may be required at multiple spatial and temporal resolutions, before settling on a single strategy.

In addition to the pathways that we have described above and in the Main Text (Figure 3), there of course exist other methods to model communities, which take into explicit account biological mechanisms such as demography, dispersal, evolution, and specialist interactions^{143,144}. We have not covered these methods because they require much more input data¹⁴⁵ and thus are limited in their applicability, although when available, all information should of course be exploited. We reiterate that species co-occurrence matrices, latent variables, phylogenetic structure, and ecological functions can all be extracted from the three statistical pathways in Figure 3, and these provide an efficient way to generate causal hypotheses for further, targeted investigation.

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